

EVIDENCE IN SUPPORT OF THE OLFACTORY
FUNCTION OF THE ANTENNÆ OF INSECTS.¹

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1. *The Present Status of the Problem.*

Investigators agree that chemotropism or the reaction of an animal to chemical stimuli plays a very important role in the biology of insects. Richardson (1) recently reviewed the extensive literature on odor as a factor in the selection of places for oviposition and in the choice of food. Odor likewise assists insects in gathering material for their nests, in detecting members of their own or "alien" species, and in bringing the sexes together.

The assignment of the sense of smell to particular organs has been beset with great difficulties. Most histologists assign the olfactory sense chiefly to the antennæ. On these organs sensillæ are found in the form of pits, cones or plate organs which are morphologically of such a nature that a chemoreceptor function has been attributed to them. Similar sensillæ may occur in other places, as on the maxillary and labial palpi, on the cerci and perhaps elsewhere, but they seem generally to be numerically greatest on the antennæ. Correlations between the number of antennal sensillæ and the habits of certain insects have disclosed a number of facts. The antennæ of Diptera that oviposit on putrid meat or feces harbor many olfactory pits whereas phytophagous forms possess few. Bloodsucking flies have many, as do those forms whose larvæ are parasitic, such as Oestrids, Bombyliids and Tachinids. The Hymenoptera possess enormous numbers of antennal sense organs. In male honey bees the number of plate organs has been computed at 30,000. In Odonata, large-eyed forms that prey on other swiftly moving insects, the number of antennal olfactory sense organs is small. Among those species where sexual dimorphism of the antennæ exists, these organs are generally more fully developed in the males than in the females. This seems to be associated with the more

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aggressive nature of the males and assists them to find the opposite sex even at great distances.

Contributions on the habits of certain moths by Forel (2) and Riley (3) and the extremely interesting deductions made from careful observations on the life of ants by Forel (2), Wheeler (4), Lubbock (5), Bethe (6), Wasmann (7), Fielde (8), and others seem to demonstrate that the antennæ serve as tactile and olfactory organs. The results of these investigators may be briefly summer up. They chiefly considered the behavior of insects when subject to various stimuli, such as the exploratory movements of the antennæ when the creatures are searching for food or for proper places to lay their eggs; the antennal movements and subsequent behavior of insects when encountering members of their own or "alien" species; the part the antennæ play when the animals are attempting to find their way to their nests and back to the forage supply; the trilling of the antennæ by males in the presence of females, etc.

Experiments to prove the above contentions are not lacking. Forel showed that certain insects which appear to find their mates by smell are unable to do so when the antennæ are amputated. Kellogg (9) showed that when one antenna is removed from silkworm moths, they always turn towards the source of odor stimulation in the direction of the remaining antenna. Barrows (10) demonstrated that *Drosophila* is unable to respond to odors when the last segment of the antennæ is removed. Von Frisch (11) trained bees to come to an odorous food supply. When the antennæ were amputated the bees could no longer find the food. In order to prove that this failure was not due to any general constitutional effects of the operation, he trained other bees to associate the food with a particular color. When the antennæ of such bees were removed they promptly found the food. Minnich (12) in some experiments on the cabbage butterfly found that the antennæ were olfactory organs but not the only ones. Most of the experimenters referred to agree that some insects will still respond, but much more slowly, to odors after the antennæ have been removed or coated with substances impermeable to volatile materials. This seems to show that olfactory organs are also located in other regions of the body.

McIndoo (13) entirely discards the view that the antennæ function as olfactory organs. This investigator has done much work on this subject and has experimented chiefly with beetles, bees and ants. McIndoo considers the abnormal behavior of insects towards odor when the antennæ are amputated, but thinks this is due to the fact that such insects are abnormal in their whole behavior. This is, of course, contrary to von Frisch's careful experiments and, if true, would apply equally to McIndoo's own work. Any animal that has been deprived of a sense organ will react abnormally with respect to a stimulation that affects this particular organ. McIndoo finds that olfactory pores exist in other regions of the body, especially at the bases of the wings and legs. When these pores are varnished over the insects respond much more slowly to odors than do those whose antennæ are amputated. Kennedy (14) recently carefully weighed the evidence for and against the antennal sense of smell and thinks that while olfactory receptors undoubtedly do occur on other parts of the body, the experimental evidence against the older theory of an antennal sense of smell is insufficient. Judging from the literature, it seems that much substantial evidence exists in favor of the older theory. However, since roaches are exceedingly favorable material for a study of this question and furnish another rather lucid illustration in support of the older view, the writer feels prompted to report some observations.

2. *Observations and Experiments on Periplaneta americana.*

Periplaneta americana, the large American roach, carries two extremely long antennæ on which occur the so-called olfactory cones. The maxillary and labial palpi of this species also bear sense organs which were, likewise, considered by Graber to function in the detection of odors. It was noticed by us that the antennæ of starved roaches moved continuously when some odorous food was tendered but held at a distance to prevent contact. This then led to the performance of some further experiments which would demonstrate whether the antennæ harbored chemoreceptors. Full grown male and female roaches were placed in an atmosphere containing a slight amount of ether vapor. After a minute or two the insects began to behave

in a curious manner. First one antenna was pushed down with the fore legs, caught near the base and rapidly passed through the mouth parts clear to the tip when it was released and the procedure repeated with the other antenna. This apparent cleaning of the antennæ continued indefinitely, or until the animals became completely anaesthetized. The maxillary and labial palps were also frequently drawn through the mouth. The same reactions occurred when carbon tetrachloride vapor or bromine was used. Two inert esters, ethyl acetate and amyl acetate (banana oil) produced identical reactions. The animals simply responded to these volatilized substances with their antennæ and palpi. No other reactions occurred until the anaesthetic effect through the spiracles became noticeable. These experiments, it seems to us, signify that chemoreceptors are located on the antennæ and on the maxillary and labial palps. This, however, does not necessarily mean that these chemoreceptors are those of smell. The reactions obtained might very easily represent merely the effect of violent chemical irritations such as the reaction of the human eye to onion oil or the reactions of the mucous membrane of the human mucosa to pollen particles. It seems unlikely, however, that two such inert substances as amyl and ethyl acetate could produce much irritation aside from exciting perhaps an obnoxious odor sensation in the insects. Nevertheless, insect sense organs are constructed differently from those of higher animals. Their surfaces, as pointed out by Kennedy, are often external and on long processes. They are also dry and consequently the direct contact with a chemical stimulus, not first dissolved in mucous secretions, may explain the differences in behavior and the reason for the great sensitivity to such stimuli. To meet the objection of simple chemical irritation and to prove that olfactory sensations are received through the antennæ some additional experiments were performed.

Two roaches with perfect antennæ were segregated in an oblong cage having a glass top and a corked hole on each of two ends. These holes were ordinarily used for the introduction of food and water. Another pair of roaches with their antennæ amputated at the base was placed in a similar cage. Each cage was completely divided in half by a double layer of a fine mesh

copper screen, producing two compartments, one for the roaches the other empty. The roaches were then held for two days to permit the operated ones to recover from the effects of the amputation. During this time they were given nothing but water in order to create an intense hunger. On the second day the insects seemed perfectly normal and a small piece of Roquefort cheese, for which these animals manifest a great fondness, was placed in the empty compartment one inch from the copper screen. In a few seconds the normal insects, which were huddled in a far dark corner, began to move their antennæ and within two or three minutes one began to move over towards that part of the screen from which the cheese odor emanated. This one waved his antennæ about near the cheese, but not being able to touch it soon returned to the corner. A little later the other roach followed the same maneuver. Both insects repeated this behavior three to four times. During the entire length of these operations, the roaches with amputated antennæ gave no response and when they moved they progressed along the side opposite the cheese which happened to be the darker side. During these tests both cages were held in the same position and at the same distance from the source of light. The cheese and the roaches were then removed and the cages washed thoroughly to remove all odors.

In a few days the roaches were again placed in their respective cages, and after the animals had been starved again for two days some Roquefort cheese was smeared on each cork plugging the hole of the compartment containing the insects. Within one to two minutes the normal roaches ran over to the soiled cork and ate off the cheese. The roaches with amputated antennæ did not respond. After more than two hours they finally came across the cheese, waved their palpi and ate. It seems that the antennæ receive smell impressions at considerable distances and that the maxillary and labial palps can only perceive an odor when the insects are in close proximity to the volatile substance. The antennæ, maxillary and labial palpi were removed from another group of roaches. After recovery from the operation, and after the customary starvation, they had even greater difficulty in finding the cheese than those

roaches with simply the antennæ amputated. They did not perceive the cheese until it was placed under their mouth parts, when they carefully tasted it before eating.

Another experiment appears significant. If the end of a stick is smeared with cheese and held at a distance of about one inch from the head of roaches with amputated antennæ nothing occurs. When the same stick is held at the same distance from the head of the normal roaches the antennæ follow the movements of the stick until they touch it, much like the pursuit of a magnet by a piece of iron. If one antenna is removed and the other left intact and the contaminated stick is held alternately on the right and left side of the head, the response occurs in about half the time on the unoperated side than on the other.

Naturally cheese is not the only substance that produces the above reactions. Dog biscuit will cause an identical response in starved roaches, but more tardily due to the much slighter odor emanating from this food.

Roaches are gregarious animals and are often found huddled together in enormous numbers. These insects emit a strong species odor rather disagreeable to humans. This odor is probably responsible for their gregarious habit. During the course of our experiments, it was noticed that those insects with the antennæ removed did not huddle as readily as was the case with the unoperated ones. After huddling the roaches with antennæ were separated by disturbing them with a prod. In approximately one-half minute they were usually found together again. Those with amputated antennæ remained separated until they accidentally ran into one another.

All of the roaches operated upon are alive up to the present (six weeks after the experiments). They behave perfectly normally in so far as their appetite is concerned and the females have deposited several egg capsules. That they are abnormal with respect to the function of smell is a foregone conclusion, but it would certainly require a stretch of the imagination to assert that they were abnormal in all their behavior.

3. Conclusions.

Chemoreceptors are located on the antennæ, maxillary and labial palps of *Periplaneta americana*. The antennæ are the most

efficient organs in detecting odor stimuli, especially from a distance. This does not imply that olfactory organs do not exist elsewhere on the body.

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